

Opinion. Opinion is intended to promote communication between lepidopterists resulting from the content of speculative papers. Comments, viewpoints and suggestions on any issues of lepidopterology may be included. Contributions should be as concise as possible and may include data. Reference should be limited to work basic to the topic.

Comments on Clench's Temporal Sequencing of Hesperiid Communities

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Competition for adult resources as a structuring force in butterfly communities was first suggested by Clench, (1967) who demonstrated the existence of five sets of hesperiid species at one locality in which competition was apparently minimized by several mechanisms. Within each set of species, the timing of adult flight period was such that the species replaced each other during the course of the summer (Figure 1). Peak populations of one (set 2) coincided with the minimum populations of another (set 1). Furthermore, at least two of the sets (1 and 2) seemed to utilize different heights of nectar sources. Thus, adult competition within each of these sets was minimal due to the sequencing of the species and competition between at least sets 1 and 2 was minimal.

Clench's data were generated over an 11-year period at the Carnegie Museum's Powdermill Preserve, and were primarily qualitative, including rough estimates of adult density, estimation of adult flight period, and observations of nectar use by each species. While his results are intriguing, there are problems in his assumptions which render his conclusions obsolete. Because of the frequency with which this paper is cited, especially in review articles, (e.g., Ehrlich, 1984; Gilbert and Singer, 1975; and Shapiro, 1975) which portray Clench's results as interesting if somewhat nebulous, a short discussion of this paper seems warranted.

Clench's main assumptions were simple: that adult hesperiid populations may be (or may have been in the past) limited by adult nectar resources, and that competitive interactions over limiting resources between species can structure communities. I agree wholeheartedly with him on these basic assumptions. My own data (Shuey, 1986) on wetland hesperiids indicate that resource partitioning is a possibility under certain conditions. Moreover, Pivnick and McNeil (1985) have recently established the importance of adult resources to one hesperiid species. Citing unpublished data, they reported that the availability of nectar increased the fecundity of *Thymelicus lineola* 27 times over that

of females which did not have access to nectar (availability of nectar could therefore have a dramatic selective impact if it was in limited supply).

Unfortunately, Clench also assumed that the community he studied had experienced the stable interactive history that would facilitate the evolution of resource partitioning. He restricted his study to hesperiids inhabiting moist to dry fields, communities that are artificially maintained in early successional states and often dominated by exotic species. The hesperiids studied (Figure 1) were mostly opportunistic species and hence unlikely to have experienced the type of pressures necessary to establish resource partitioning via past competition. Clench's admission that his temporally distributed species sets did not exist 200 miles east of his study site (despite the absence of any obvious barriers to gene flow for the hesperiids in question) indicates that these sets may be artifacts of other factors such as host plant phenology

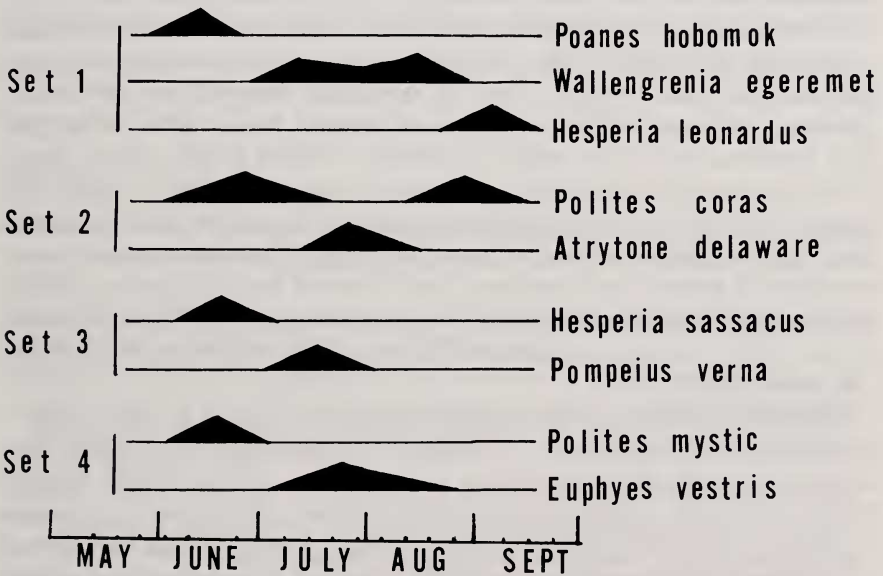


Figure 1. The average flight periods of Clench's (1967) Hesperinae sets 1 to 4. Relevant to his arguments are the "temporal replacement of the members within each set, and the coincidence of the peaks of Set 2 with the intervals (population minima) of Set 1." The species in set 1 were the largest and most common during his study and had a "decided preference" for tall flowers. The species of set 2 generally fed on low-growing flowers but had "been observed at times on tall flowers, suggesting a certain degree of active competition with set 1 species." The remaining sets showed no cohesive nectar source preferences. A fifth set composed of *Polites themistocles* and *Polites origenes* was present but too rare for Clench to present data. (Redrawn with permission from Clench, 1967).

(Slansky, 1974) in conjunction with the length of the developmental season (Shapiro, 1975). Both of these external factors are known to affect the period of adult activity, and any explanation of adult flight periods which fails to incorporate or account for these factors is partial at best. For example, in one of the species, *Wallengrenia egeremet* (Scudder), latitude nicely explains the phenology of broods (Burns, 1985).

To date, evidence accumulated for or against competition as a structuring force in communities has utilized taxonomically diverse assemblages of species inhabiting geographically widespread and ecologically diverse communities (Schoener, 1983; Strong, 1984). Given the assumptions which underlie the premise of a structured community (i.e., stable gene frequencies controlling behavioral and morphological traits) it is unrealistic to expect to find resource partitioning in widespread, panmictic populations occupying ecologically diverse areas which vary with respect to the pool of potential competitors. Better communities for this type of investigation are those which are associated with rare and/or fragmented abiotic conditions (i.e., communities containing populations with very little or no genetic influx from other populations), and whose array of potential competitors are homogeneous. Representative communities include those found in serpentine barrens, bogs, fens, alpine meadows, natural ponds, and so forth. The most suitable potential competitors for this type of study are groups of closely related species, increasing the potential for competition due to similar ecological requirements. Examples of such communities of species are numerous, and among the lepidoptera include *Heliconius* butterflies (Gilbert, 1984), checkerspot butterflies (Ehrlich, *et. al.*, 1975), wetland hesperiids (Shuey, 1985), and prairie *Hesperia* (McGuire, 1982).

If potential resource partitioning is identified I feel it is more likely *a priori* to be the result of; 1) random circumstances; 2) localized continuous interspecific competition for resources within closed populations; or 3) the spread of formerly localized populations in which resource partitioning had become genetically fixed during a past period of localized interspecific competition. Each of these scenarios makes predictions testable under field conditions using closed natural communities. If the apparent resource partitioning is the result of random or haphazard circumstances, observations upon several communities should reveal random patterns of resource partitioning including communities which demonstrate no partitioning. If resource partitioning is the result of localized continuous interspecific competition a series of communities should demonstrate various combinations of resource utilization patterns. (i.e., there should be several independent solutions to the resource partitioning problem which would superficially resemble random or haphazard patterns, but with all communities demonstrating resource partitioning). If the apparent resource partitioning

developed at sometime in the past and was genetically fixed before the current range of the species was occupied, all of the communities should show the same answer to the resource partitioning problem.

While no research directly addresses these predictions, the few available studies of closed or nearly closed communities indicate that such work is feasible and likely to yield important results (Schoener, 1974, 1983). By quantitatively assessing the spectra of adult resources used under various "natural" combinations of potential competitors, baseline patterns can be documented for direct comparison. Once baseline data is in place, some types of communities are ideally suited for the introduction of "missing competitor(s)" to test for competition (e.g., small wetlands where appropriate host plants are usually present, and the missing potential competitor[s] usually occur nearby). The resulting shifts, or lack thereof, in the spectra of resources used after the introduction (assuming the proper control communities are maintained), should shed light on the basic question at hand: are the observed ecological differences between species the result of competitive interactions or are they the result of other biotic or abiotic factors?

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